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Notes on the Cerebral Convolutions of the Carnivora.

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In the year 1834, Sir Richard Owen, in describing * the brain of the Cheetah (*Felis* (*Cynælurus*) *jubata*), took occasion to point out the generally similar disposition of the cerebral convolutions throughout the feline group. The subject has been further treated by him in his 'Anatomy of Vertebrates' †. Considerably before the appearance of the last-named work, MM. Leuret and Gratiolet published descriptions, with admirable illustrations ‡, of the convolutions of a variety of carnivorous mammals, pointing out the characters which are more or less common in, or are peculiar to, four sets of species. M. Dareste also contributed a memoir § on the convolutions of the mammalian brain, one section being devoted to "Types des Carnivores." The late Professor Paul Gervais published ‖, later on, an account of the same structures in a much greater number of carnivorous species, accompanied by numerous figures representing the brains of such species and of

* See Trans. Zool. Soc. vol. i. pp. 133–136, plate xx.

† See vol. iii. p. 116 (1868).

‡ 'Anatomie Comparée du Système nerveux,' with an Atlas (1839–1857).

§ "Circonvolutions du Cerveaux chez les Mammifères," in the Ann. des Sc. Nat. 4e série (1855), tome iv. pp. 73–76, plate ii. figs. 1–8.

‖ "Mémoire sur les formes cérébrales propres aux Carnivores," Nouvelles Archives du Mus. vol. vi. (1870), pp. 103–162, plates iii.–ix.

casts of the interiors of their skulls. A little later, Professor Burt Wilder further elucidated the subject by a paper * giving an account of the cerebrum, with figures, of many varieties of Dogs, as well as of that of *Hyæna*, *Ursus*, and *Procyon*, together with some feline species. In 1880, Julius Krueg † gave forth an elaborate memoir largely on the same subject, by far the most elaborate and complete which has yet appeared, and to which frequent reference will be made. The following year Professor Burt Wilder read before the American Philosophical Society ‡ an elaborate paper on the brain of the Cat—a paper which has its place on the shelves of our Library. Last of all, Mr. Langley has given us § a very complete paper on the brain of the Dog, wherein will be found || references to yet other memoirs relating to the physiology of the subject and to questions of the cerebral homologies of different orders of mammals—questions with which this paper is not concerned.

I am not aware of any other works on the subject than those here directly, or, as above, indirectly, referred to; but there are various isolated descriptions of the brain of different carnivorous mammals, such as those of the late Professor Garrod and of Professor Flower, which will be referred to when the subjects they treat of come to be mentioned. Three of these, however, may be referred to at once ¶, since in them the two Professors give a short summary of such cerebral characters as they believe to be common to the main subdivisions of the Fissipedal Carnivora.

My object in this paper is to point out the leading cerebral characters of many genera of Carnivora, and especially those of certain forms which appear either not to have come under the direct observation of the before-mentioned authors, or not to have had certain characters described which it seems to me desirable to note. I purposely confine myself to the observation of a few characters which I believe to be leading characters, having had

* In the 'Proceedings of the American Association for the Advancement of Science,' 22nd Meeting (Portland, Maine, August 1873), pp. 214–234.

† "Ueber die Furchen auf der Grosshirnrinde der Zonoplacentalen Säugethiere," Siebold's Zeitschrift f. wissen. Zool. vol. xxxiii. (1880), pp. 595–648, plates xxxiv.–xxxviii.

‡ On July 15th, 1881.

§ In the 'Journal of Physiology,' vol. iv. pp. 248–285.

|| At page 276.

¶ Namely, two papers by Professor Flower, in P. Z. S. 1869, p. 482, and P. Z. S. 1880, p. 73; and one by Professor Garrod, P. Z. S. 1878, p. 375.

forced on me a conviction of the great variability of the more minute details of cerebral conformation. As Professor Burt Wilder remarks *, when the brains of two or three individuals are alone examined, it is easy enough to draw out distinctive characters, many of which, however, a more extended survey soon shows to be worthless. I have been greatly impressed, not only with the variability in the details of the gyri in the same species, but even with the differences which every now and then present themselves in the two sides of the brain of the very same individual. Nevertheless, in spite of the great variability referred to as to matters of detail, I am convinced that the characters on which I lay stress have a taxonomic value, and some of them appear to me also to possess a certain phylogenetic interest and significance.

Cynoidea.

The brains, not only of all Dogs, but of all the animals which together constitute the suborder Cynoidea†, are as a rule singularly uniform as regards those points of structure with which the present paper is concerned. I have examined the brains of various domestic Dogs, of the Fox, Jackal, the common Wolf, the Red Wolf, *Canis Azaræ*, *C. microtis*, and the singular Raccoon-like Dog, *C. procyonoides* (type of the proposed genus *Nyctereutes*), as also of *Icticyon venaticus*, *Lycaon pictus*, and *Otocyon megalotis*, availing myself in the study of this, as of every other group, of the rich and yearly increasing stores preserved in the Museum of the Royal College of Surgeons.

The cerebral characters which have been pointed out before as common to the Canidæ I have found uniformly present, save

* Proc. of Amer. Assoc. for the Advancem. of Sci. p. 233. He says:—"After a pretty careful study of the specimens and works at my command, I feel justified in asserting that we cannot as yet characterize the fissural pattern of any Mammalian order, family, genus, or even species without the risk that the next specimen will invalidate our conclusion." He advocates, p. 232, a study of the variation presented by the two sides of the brain of the same individual in order to obtain "a test of the value of the differences observed amongst brains." Such a study might be thus useful; but it does not come within the scope of the present paper.

† See Leuret, *l. c.* vol. i. pp. 373–378, plate iv.; Dareste, *l. c.* p. 74, fig. 1; P. Gervais, *l. c.* pp. 107–119, plates i., ii., and figs. 1–7, plate iii.; Burt Wilder, *l. c.* pp. 214–248, with many figures of varieties, plates i.–v.; Krueg, *l. c.* pp. 612–617, plate xxxiv.; and Langley, *l. c.* pp. 248–280, woodcuts, figs. 1–3, and plates vii. & viii.

on one side of the brain of one species. In every case the Sylvian fissure is embraced by four successive circum-Sylvian convolutions, which, for my present purpose, I shall distinguish by four simple designations. The two lowest gyri I shall distinguish as the *Sylvian* gyri (a term already in use), that next the Sylvian gyrus being called the *first* and the adjoining one above, the *second* Sylvian gyrus. The third gyrus from the Sylvian fissure I shall designate the *parietal gyrus*, and the next, and uppermost one, will be spoken of as the *sagittal gyrus*, since it lies in close proximity to the sagittal crest and suture. In every case I found the two Sylvian sutures well separated and distinct, save on one side of the brain of *Icticyon venaticus*, where the posterior limb of the first Sylvian gyrus was rudimentary *. Professor Burt Wilder, however, figures seven instances in which he found the separation between the Sylvian gyri incomplete in domestic Dogs †. In every case, without exception, I found the posterior limb of the parietal gyrus to be subdivided by a longitudinal sulcus, so that it bifurcated backwards. Prof. Burt Wilder observes that this bifurcation sometimes extends to the anterior end of the parietal gyrus ‡.

In every case I find that there is, on the inner surface of each cerebral hemisphere, a direct continuation of the calloso-marginal sulcus into the crucial sulcus, thus cutting off what is known as the hippocampal gyrus from the sagittal gyrus. In no case do I find, when the dorsum of the brain is looked at, that there is any sulcus proceeding forwards and inwards in front of the crucial sulcus of one hemisphere towards a similarly situated sulcus in the other hemisphere. Nothing of the kind is indicated in any figure of a Cynoid brain which I have seen. Sometimes (as I find in *C. Azaræ*, *C. microtis*, and *Lycaon pictus*) the sagittal gyrus is longitudinally grooved, as is also its inner side in *Lycaon* and some domestic Dogs.

* ...ly noted by Professor Flower in his paper on the anatomy of that ...73–76, figs. 6 & 7. The number of this speci... tions in the Museum of the Royal ...

...hound, and 20 to 24, Pomeranian Dogs (the animal the brain of which is represented in fig. 20 being the mother of those the brains of which are represented in figs. 21, 22, & 23), and, lastly, fig. 25, an English Terrier.

‡ *L. c.* p. 231, and the figures 12, 21, and 22.

Felidæ.

A similar but different uniformity prevails amongst the extensive group of Cats *, whether of the largest or smallest species though, as has been again and again remarked, the larger the species the more convoluted the gyri; especially is this the case with the fourth or uppermost gyrus. Small bridging convolutions have been observed † connecting the sagittal and parietal gyri. They, however, are very inconstant; but there is a constant, more or less extensive connection between the parts answering to the two Sylvian gyri of the Dog. Thus in every Cat there is a very broad gyrus next the Sylvian fissure, either limb of which is grooved by a more or less vertical sulcus, which is the rudimentary representative of the sulcus which completely separates the two lowest circum-Sylvian gyri of the Dog. The second distinguishing character common to the whole of the Felidæ, so far as I have been able to observe, is the non-bifurcation (or subdivision by a longitudinal groove) of the parietal gyrus. The third universal character is the continuation of the hippocampal gyrus forwards and upwards to blend, behind the crucial sulcus, with the sagittal gyrus, the hinder end of the crucial sulcus being thus separated off from the anterior end of the calloso-marginal sulcus by the ascending bridge of convolution from the hippocampal gyrus. Sometimes the, always very conspicuous, crucial sulcus is placed very far forwards ‡. It is always simple, as in the Dogs.

The genera which compose the other families of Carnivora differ so in the details of their cerebral structure as to demand separate notice.

Viverra.—The Civet § has the parts which answer to the two lowest circum-Sylvian gyri of the Dog still more completely blended together than they are in the Cats. The single Sylvian

* See Leuret, *l. c.* vol. i. p. 378, plate v.; Dareste, *l. c.* p. 74, figs. 3 & 4; and P. Gervais, *l. c.* p. 119, and plate ix. fig. 7. See 'The Cat' (published by John Murray), pp. 268 & 269, figs. 125, 126, 127. "The Brain of the Cat," by Professor Burt Wilder, a paper read before the American Phil. Soc., July 15th, 1881, four plates; also Krueg, *l. c.* pp. 547–622, and plate xxxv.

† By MM. Leuret and Gratiolet.

‡ As in the Cheetah. See P. Gervais, *l. c.* plate ix. fig. 7, and Owen, Trans. Zool. Soc. vol. i. plate xx.

§ See Leuret, *l. c.* p. 378; P. Gervais, p. 128, pl. ix. fig. 5. See also P. Z. S. 1882, p. 516; Krueg, *l. c.* p. 625, plate xxxvi.

gyrus thus formed has its pre-Sylvian limb sometimes much broader, sometimes narrower than that behind the Sylvian fissure, and it is more or less vertically grooved, the groove being a remnant of that sulcus in the Dog which separates its first and second Sylvian gyri one from the other. The gyrus next above the parietal gyrus (answering to the third from the Sylvian fissure of the Dog) is simple, and not only differs from the corresponding gyrus of the Dog in being undivided, but also in being shorter, the sulcus between it and the sagittal gyrus not extending so far backwards. The hippocampal gyrus is separated off from the sagittal by the continuation forwards and upwards of the calloso-marginal sulcus, as in the Dogs. The most striking difference presented by the upper surface of the Civet's cerebrum, when compared with the cerebrum of any of the Carnivora here before referred to, is the minute size of the crucial sulcus—a sulcus so conspicuous in all the Felidæ and Canidæ. It is with this minute crucial sulcus that the calloso-marginal sulcus unites.

Genetta.—The Genet's * brain is like that of the Civet, still further simplified. It agrees with the latter save that the Sylvian gyrus shows less traces of its subdivision into two circum-Sylvian gyri than in the Cats (the single Sylvian gyrus being almost smooth), and that the crucial sulcus is much more rudimentary still, being only indicated, on the dorsal surface of the cerebrum, by a minute notch.

Nandinia.—The brain of this exceptional form † is quite like that of *Genetta*, save that the Sylvian gyrus more resembles the same part in *Viverra*.

Paradoxurus.—The brain of the palm-Cats ‡ has the hinder limb of the Sylvian gyrus twice the size of its anterior limb, and marked by a vertical groove, which indicates that both the first and second of the Sylvian gyri of the Dog are represented behind the Sylvian fissure, while only one of these canine gyri is represented in front of it. As in the Civet and Genet, the hinder part of the parietal gyrus is short, blending posteriorly and inferiorly with the sagittal gyrus behind the hinder end of the shortened

* See Leuret, *l. c.* p. 381 ; P. Gervais, p. 128, plate vii. fig. 5. See also P. Z. S. 1882, pp. 515 & 516, fig. 11 ; Krueg, *l. c.* plate xxxvi.

† As to its peculiarities, see P. Z. S. 1882, p. 169.

‡ See P. Gervais, *l. c.* p. 129, plate ix. figs. 2, 2*a*, 2*b*, & 2*c* ; and Krueg, *l. c.* plate xxxvi.

sulcus between them. The crucial sulcus is altogether absent from the cerebral surface; nevertheless the calloso-marginal sulcus is continued forward to the place where the crucial sulcus exists in most Carnivora, thus separating the hippocampal and sagittal gyri behind that point. The brain of *Hemigalea* agrees with that of *Paradoxurus*.

Arctictis.—The Binturong * has a brain similar to that of *Paradoxurus*, save that the sagittal and parietal gyri are separated posteriorly for a longer space, that the crucial sulcus is distinct though small, and that the sagittal gyrus is complicated by certain additional depressions.

Cynogale.—The brain of this animal is only known to me by Professor P. Gervais's figure of the cast of the inside of its skull †, which shows the cranial convolutions with exceptional distinctness. There is no crucial sulcus. The parietal sulcus, like that of every carnivorous animal not of the Dog group, does not bifurcate posteriorly. The hinder limb of the Sylvian gyrus shows no indication of subdivision, and the Sylvian fissure is described as "*longue et oblique en arrière*." The most marked peculiarity of this brain is the great expansion of the parietal gyrus at its anterior end, this expanded part being longitudinally grooved with short secondary grooves radiating from the longitudinal one.

Eupleres.—This very exceptional and insectivorous-like Carnivore ‡ is unfortunately, so far as I know, undescribed, save as regards the cast of the interior of the skull §. It appears to have the Sylvian gyrus formed as in *Paradoxurus*. There is no crucial sulcus visible, and the parietal gyrus does not bifurcate posteriorly. The most striking character shown by the figure of this cast is the very great breadth of the sagittal gyrus.

Herpestes.—The Mongooses have been placed in a category by themselves, as regards their cerebral structure, by MM. Leuret and Gratiolet ‖, on account of the apparently anomalous complexity of structure presented by at least some forms of this extensive genus. There appear to be sometimes as many as five

* See P. Gervais, p. 129, and plate vii. fig. 13, which represents a cast of the inside of the skull. See also P. Z. S. 1882, p. 516; but see especially Garrod, P. Z. S. 1873, p. 201, where a view of the side of the brain is given.

† See *l. c.* p. 128, plate vii. fig. 8.

‡ For its peculiarities, see P. Z. S. 1882, p. 189.

§ See P. Gervais, *l. c.* p. 130, pl. vii. fig. 2.

‖ See *l. c.* p. 383.

circum-Sylvian convolutions, so that the Ichneumons seem to exceed even the Dogs in their wealth of convolutions. In fact, however, not only is there no really special resemblance between the brains of *Herpestes* and *Canis*, but the brain is less convoluted than might appear from what has been said; for all the convolutions are narrow, single, longitudinal, and tend to be imperfectly separate one from another, especially towards the hinder part of the cerebrum *.

In some species the Sylvian gyrus is more or less subdivided both in front and behind the Sylvian fissure, and in others the sagittal gyrus is divided by a more or less extensive longitudinal groove. Thus it is that there may appear to be three, four, or even five circum-Sylvian gyri. The parietal gyrus, however, is never posteriorly subdivided as in the Dogs. One very marked character which distinguishes the brain of *Herpestes* from the brains of *Nandinia*, *Paradoxurus*, *Arctictis*, *Cynogale*, and *Eupleres* is its large crucial sulcus, which is always plainly to be seen, often rather forwardly situated, on the dorsum of the cerebrum. Into this sulcus the calloso-marginal sulcus is continued forwards, separating the hippocampal and sagittal gyri, as they have always been separated in all the species we have yet considered, except the species of Felidæ.

Galidia.—The brain of this elegant little genus is a simplified Herpestine brain, there being † but three circum-Sylvian gyri with a very large and conspicuous crucial fissure. The hinder limb of the Sylvian gyrus is vertically grooved.

Crossarchus.—The brain in this genus bears a large crucial sulcus, into which the calloso-marginal sulcus is continued. The Sylvian gyrus has its hinder limb twice as broad as its anterior limb, and the former is furrowed by a longitudinal vertical groove.

Suricata.—The Suricate ‡ has a brain which is remarkable for the great size of that part of the Sylvian gyrus which is posterior to the Sylvian fissure. This fissure has the appearance of being prolonged upwards, and then suddenly and much curved backwards and downwards, causing that part of the Sylvian gyrus

* See P. Gervais, *l. c.* p. 132, and plates vi. fig. 10, vii. fig. 4, viii. figs. 6 & 7, and ix. fig. 1. See also Krueg, *l. c.* plate xxxvi.

† See P. Gervais, p. 131, pl. vii. fig. 3.

‡ See P. Gervais, *l. c.* p. 133, pl. viii. figs. 5 and 5*a*; see also Krueg, *l. c.* pl. xxxvi.

which morphologically is behind the fissure to be actually in front of its distal portion. Behind this apparently recurved end of the fissure, there is a vertical groove on the middle of the Sylvian gyrus, which is thus altogether extremely broad posteriorly. The sagittal gyrus is longitudinally grooved at its hinder part, and there is a relatively large crucial sulcus, into which, no doubt, the calloso-marginal sulcus is duly continued.

Hyæna and Crocuta.—The brain of the Hyænas* shows a rather prolonged Sylvian fissure, while the posterior limb of the Sylvian gyrus is twice the breadth of its anterior limb, and is vertically grooved, and may be doubly grooved, so that the Sylvian fissure may seem to be posteriorly recurved. There is a very large crucial sulcus, into which the calloso-marginal sulcus is prolonged on the inner face of each hemisphere. The parietal shows no tendency to the canine bifurcation.

Proteles.—The brain of this singular animal † presents all the essential characters of that of the Hyænas.

Cryptoprocta.—I am indebted to the kindness of Professor Alphonse Milne-Edwards for a sketch of the brain of this animal, which is only otherwise known by a cast of the interior of its skull ‡. The crucial sulcus is distinct, though rather small, and anteriorly situated. The parietal and sagittal gyri communicate towards the hinder end of the cerebrum. The Sylvian gyrus appears to resemble rather that of the Hyænas, its posterior limb being double the width of its anterior limb, and obliquely grooved from above downwards. This groove, however, seems, by the drawing, to join above the upper part of the Sylvian fissure, which has thus an appearance of being recurved, as it has in the Suricate. It may be, however, that the Sylvian gyrus is very short and embraced by two distinct Sylvian gyri, as it is in the Dogs. If this is not the case, then the Sylvian gyrus is like that of *Herpestes*, *Crossarchus*, *Suricata*, and the Hyænas; while the connection between the parietal and sagittal gyri is a character which reminds us of the Felidæ. There is certainly no special resemblance to the *Viverrinæ*.

The non-canine and non-feline forms hitherto reviewed appear to present the following affinities :—In the first place their brain differs from that of the Cats by the non-continuance of the

* See Leuret, *l. c.* p. 378 ; and P. Gervais, *l. c.* p. 119, pl. ix. fig. 11 (brain of *Crocuta*); see also Krueg, *l. c.* pl. xxxvi., and Burt Wilder, *l. c.* fig. 9.

† See Flower, P. Z. S. 1869, pp. 478–482, figs. 1–4 ; and Krueg, *l. c.* pl. xxxvi.

‡ See P. Gervais, *l. c.* p. 123, pl. vi. fig. 2.

hippocampal into the sagittal gyrus behind the place of the crucial sulcus. Secondly, they differ from the Dogs in the non-bifurcation posteriorly of the parietal gyrus. Thirdly, they all agree together with both the Canidæ and Felidæ in not having any complication of the crucial sulcus by the extension of subordinate sulci forwards and inwards in front of its anterior margin.

The non-canine and non-feline species here considered—all of which belong to the non-feline portion of the suborder Æluroidea—divide themselves, as regards their cerebral structure, into two marked groups. To one of these belong the genera *Viverra*, *Genetta*, *Nandinia*, *Paradoxurus*, *Arctictis*, *Cynogale*, and *Eupleres**, which all (so far as I have been able to observe) differ from other Carnivora by the abortion, or quite rudimentary condition, of the crucial sulcus. Contrasted with these are the Æluroid genera *Herpestes*, *Galidia*, *Crossarchus*, *Suricata*, *Hyæna*, *Crocuta*, *Proteles*, and *Cryptoprocta*, all of which agree in having a well-developed crucial sulcus and a Sylvian gyrus, the hinder limb of which is twice or more (except sometimes in *Herpestes*) the breadth of its anterior limb, and bears a vertical groove.

We come now to the series of forms which constitute the Arctoid group of the Carnivora.

Procyon.—The brain of the Raccoon †, like that of all the forms which have hereinafter to be noticed, has three circum-Sylvian gyri, whereof the parietal gyrus does not bifurcate posteriorly, thus differing from the Canidæ. The Sylvian gyrus has its anterior limb much smaller than its posterior limb. The parietal gyrus is large, expanding anteriorly, becoming considerably contorted, and sometimes communicating, by a bridge of convolution, with the sagittal gyrus. The sagittal gyrus is very large, and becomes complicated anteriorly. This I find to be especially the

* Thus the cerebral structure justifies the affinities and classification of the Æluroids which I indicated in my paper on that group (in the Proc. Zool. Soc. 1882, p. 135), except as regards *Eupleres*, which I associated rather with the Ichneumons than with the Civets. It is interesting to note the evidence afforded by the brain of the affinity between the Hyænas and the Ichneumons. Professor Flower had already remarked (P. Z. S. 1869, p. 482, note §) the greater resemblance of the brain of the Suricate to that of the Hyænas than to that of the Civets.

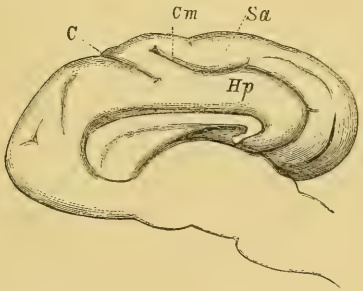
† See P. Gervais, *l. c.* p. 141, pl. viii. fig. 1; Krueg, *l. c.* pl. xxxvii. p. 633; and Burt Wilder, *l. c.* pl. ii. fig 11.

case in the brain of *P. cancrivorus*, where there are two or three bridging convolutions, on each side, between the parietal and sagittal gyri. In *Procyon* we find once more what we have found hitherto only in the Felidæ, namely, a continuation of the hippocampal gyrus upwards into the sagittal gyrus, behind the crucial sulcus, the calloso-marginal sulcus not being continued forwards with the latter. The crucial sulcus is very large and distinct, and presents a character which I have not found to exist in the brain of any non-Arctoid Carnivore. From the anterior margin of the crucial sulcus of either hemisphere a secondary sulcus diverges forwards and inwards, and thus the proximal parts of the two halves of the great crucial sulcus, together with the secondary and anteriorly approximating sulci, form altogether a lozenge-shaped patch of brain-substance which is sufficiently conspicuous.

The Sylvian fissure is very elongate and very oblique.

Nasua.—The brain of the Coati * is mainly like that of the Raccoon; but the part in front of the large crucial sulcus is relatively more extensive, and the sagittal gyrus is larger and more complicated with grooves and depressions. One great difference, however, between the two brains is the small size in *Nasua* of the

Fig. 1.



Vertical median section of cerebrum of *Nasua rufa*, nat. size.

C. Crucial sulcus. *Cm.* Calloso-marginal sulcus. *Hp.* Hippocampal gyrus. *Sa.* Sagittal gyrus.

lozenge-shaped patch of brain-substance in front of the crucial sulcus. The fact that minute secondary sulci do converge forwards from the crucial sulcus, I have been careful to verify by a special examination of a brain freshly extracted for the purpose.

* See Leuret, *l. c.* p. 381, pl. vi.; and P. Gervais, *l. c.* p. 140, pl. ix. fig. 10; also Krueg, *l. c.* pl. xxxvii.

They are, however, very minute, and more or less hidden under the fold of cerebrum which overhangs the crucial sulcus posteriorly. I have also ascertained that the calloso-marginal sulcus does not attain the crucial sulcus, so that the hippocampal and sagittal gyri join below the former sulcus.

Ailurus.—The brain of the Panda * is well represented in the Museum of the Royal College of Surgeons. The anterior limb of the Sylvian gyrus is but little wider than its posterior limb. The latter is marked by a secondary sulcus, which descends from the hinder margin of the elongated Sylvian fissure, producing the appearance of a recurvation of that fissure—an appearance already noted in the brain of *Suricata* and *Hyæna*. In other respects the cerebrum much resembles that of *Procyon*, save that there is a feebler indication of the lozenge-shaped patch of brain-substance in front of the large crucial sulcus. Behind that sulcus, the hippocampal gyrus joins with the sagittal one, as in *Procyon* and *Nasua*.

Ailuropus.—I have not seen the brain of this very interesting form, but only a mould of the interior of the skull †. The brain is evidently short and broad, with a very large crucial sulcus, which gives off in either hemisphere a secondary sulcus proceeding inwards and forwards, and so defining a large and conspicuous lozenge-shaped tract of brain-substance, which is larger (relatively as well as actually) in this somewhat bear-like animal than in the preceding Arctoid species. I shall henceforth speak of this cerebral patch as the "*Ursine lozenge*." The Sylvian fissure is very long and placed very obliquely. The Sylvian gyrus has its anterior limb much the narrower. The anterior limb of the sagittal gyrus is very large and very much convoluted.

Bassaris.—The cranial characters of this much-disputed genus have already abundantly proved that it is no Viverrine animal, but belongs to the great Arctoid group. (Prof. P. Gervais's figure of a cast ‡ of the interior of the skull is the least satisfactory and instructive of his whole series.) Nevertheless, the existence of a large crucial sulcus would alone be a strong argument against its having an affinity to the Civets. It seems

* This is noticed by P. Gervais, *l. c.* p. 141, and he figures (pl. viii. fig. 8) a mould of the inside of the skull. The brain itself is described and figured by Professor Flower, Proc. Zool. Soc. 1870, pp. 755–757, figs. 1, 2, & 3.

† See P. Gervais, *l. c.* p. 136, pl. viii. fig. 9.

‡ See *l. c.* pl. vii. fig. 6; for a notice see p. 140.

generally, as might be expected, to show a resemblance to the brains of *Procyon* and *Nasua*, though it is less convoluted. It shows a long Sylvian fissure embraced by a simple Sylvian gyrus.

By the kindness of Professor Flower and Dr. Günther I have been enabled myself to obtain a cast of the interior of the skull of this animal, which cast I have deposited in the British Museum, South Kensington. Unfortunately it shows but little of the convolutions, but the size and forward position of the crucial sulcus agree with Gervais's figure. There is no positive indication, that I can perceive, of an "Ursine lozenge," though there is no evidence against its presence, the part being indistinct. The sagittal gyrus is exceedingly wide, and complicated by a median longitudinal groove.

Bassaricyon.—It is again through the kindness of Professor Flower and Dr. Günther that I am enabled to contribute any notes as to the cerebral form of this species. It is as yet entirely unknown; but I have been allowed to take a cast from the interior of the skull, which cast I have also presented to the British Museum. By it, it seems that there is a very large crucial sulcus, not placed so far forwards as in *Bassaris*. On one side there is a distinct indication of the presence of an "Ursine lozenge." The sagittal gyrus seems to be very broad, but the indications are unfortunately very indistinct. There is an appearance which seems to show that the anterior limb of the Sylvian gyrus is narrower than its posterior limb.

Cercoleptes.—The brain of the Kinkajou * is short and somewhat rounded. Its sagittal gyrus is very wide, and tends to subdivide longitudinally. The parietal gyrus broadens out much anteriorly. The Sylvian fissure is long and oblique, and its embracing Sylvian gyrus has its anterior limb a little narrower than its posterior limb. Professor Gervais says that he found no "plis de passage;" but I find a bridging convolution anteriorly, on each side, between the parietal and sagittal gyri. The crucial sulcus is very large, and sends inwards, on either side, a rather faintly marked secondary sulcus, by which a large "Ursine lozenge" is distinctly, though not strongly, defined. The crucial sulcus is joined by the anterior end of the calloso-marginal sulcus, thus cutting off the hippocampal gyrus from the sagittal one †.

* See P. Gervais, *l. c.* p. 141, pl. ix. fig. 3; and Krueg. *l. c.* pl. xxxvii.

† See Leuret, *l. c.* p. 381; and P. Gervais, p. 144, pl. ix. fig. 6.

*Meles**.—I find that the Sylvian gyrus has its anterior limb the narrower, and the parietal gyrus single both in front and behind. The sagittal gyrus, on the contrary, expands very much forwards and is very contorted, and has certain superficial linear depressions on its more posterior part. The anterior part of the cerebrum is very largely developed, the crucial sulcus being placed very far back. A small, but very distinct, secondary sulcus extends forwards and inwards in either hemisphere from very near the middle line of the crucial sulcus. Thus a very small Ursine lozenge is formed, but one which is at the same time very definite and distinct. I have had no opportunity of ascertaining whether the calloso-marginal sulcus is continued forwards on to the crucial sulcus, but it is represented as so doing by Krueg.

Mellivora.—The brain of the Ratel is referred to by Professor

Fig. 2.

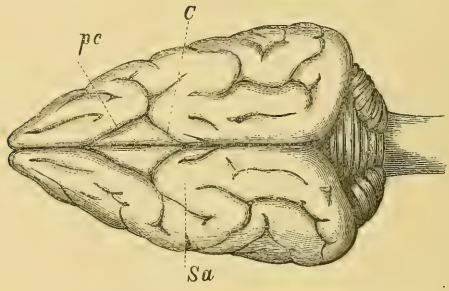


Fig. 3.

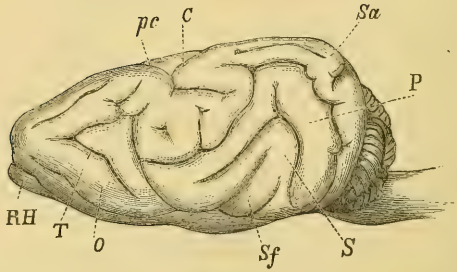


Fig. 2. Dorsal surface of brain of *Mellivora indica*, natural size. *C.* Crucial sulcus. *pc.* Precrucial sulcus. *Sa.* Sagittal gyrus.

Fig. 3. Right side of brain of *Mellivora indica*, natural size. *C.* Crucial sulcus. *O.* Orbital gyrus. *P.* Parietal gyrus. *pc.* Precrucial sulcus. *RH.* Rhinencephalon. *S.* Sylvian gyrus. *Sf.* Sylvian fissure. *Sa.* Sagittal gyrus. *T.* T-shaped sulcus.

* See Krueg, *l. c.* pl. xxxvii.

P. Gervais *, but is neither described nor figured by him, nor do I know of any published representation of it. The Sylvian fissure is long and oblique. The Sylvian gyrus is very much broader posteriorly, the anterior limb being exceedingly narrow. The parietal gyrus is quite simple, and its anterior and posterior limbs are about equal. The sagittal gyrus is enormously expanded anteriorly. Its most posterior part is quite simple and single, but behind the crucial sulcus it is longitudinally grooved. It then doubles backwards and afterwards curves forwards in complex convolutions, surrounding the crucial sulcus. The latter, which is well developed, sends forwards secondary sulci, and so forms a rather elongated "Ursine lozenge."

The supraorbital gyrus (fig. 3, *O*) is large, and bears a T-shaped or Y-shaped vertical sulcus (*T*).

The calloso-marginal sulcus does not join the crucial one, but a very narrow bridging convolution connects the hippocampal and sagittal gyri behind the crucial sulcus.

Galictis †.—In the Tayra, the part of the cerebrum which is anterior to the crucial sulcus is smaller than in *Mellivora*. The upper surface of the brain is singularly complicated by supplementary depressions, and by bridging convolutions which connect the parietal and sagittal gyri, so that it is very difficult to determine which gyrus of the two is the one which is the more broadened and complicated anteriorly. Indeed, it seems impossible to draw any well-defined boundary between them. The Sylvian fissure is oblique and prolonged. The Sylvian gyrus is simple, and has its anterior limb very decidedly the narrower. The parietal gyrus, if it could be considered simple, must be said to blend with the sagittal gyrus by several bridging convolutions. The sagittal gyrus must then be considered as very wide, and as bearing two longitudinal grooves at its middle part. It blends, as just stated, with the parietal sulcus, and expands widely as it advances forwards. Its hindmost part is very broad, and bears a median longitudinal groove. The crucial sulcus sends forwards, on either side, a groove to define a small "Ursine lozenge." It is not joined by the calloso-marginal sulcus, a bridging convolution connecting the hippocampal and sagittal gyri behind the crucial sulcus.

* See *l. c.* p. 145.

† Referred to by P. Gervais, *l. c.* p. 144. He gives no figure.

Fig. 4.

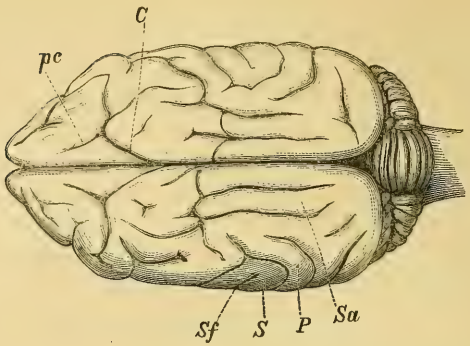


Fig. 5.

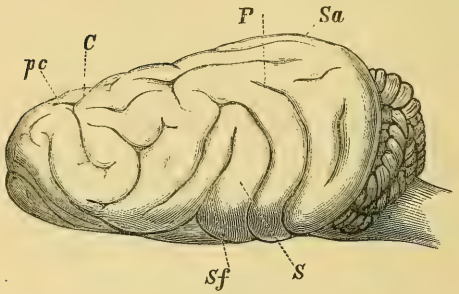


Fig. 4. Dorsal surface of brain of *Galictis*, natural size. *C.* Crucial sulcus. *P.* Parietal gyrus. *pc.* Precrucial sulcus. *S.* Sylvian gyrus. *Sa.* Sagittal gyrus. *Sf.* Sylvian fissure.

Fig. 5. Lateral view of brain of *Galictis*, natural size. *C.* Crucial sulcus. *P.* Parietal gyrus. *pc.* Precrucial sulcus. *S.* Sylvian gyrus. *Sa.* Sagittal gyrus. *Sf.* Sylvian fissure.

Grisonia *.—The brain of the Grison is so different from that of the Tayra (*Galictis*) as to constitute an argument of some weight in favour of the distinctness of the two genera. In that of the Grison, the hippocampal gyrus is cut off from the sagittal gyrus by the junction of the calloso-marginal and crucial sulci. There is also a much larger proportional part of cerebrum in front of the crucial sulcus in *Grisonia* than is the case in *Galictis*. The sagittal gyrus is very wide, and blends anteriorly with the parietal gyrus. The Sylvian gyrus is oblique and rather short.

The crucial sulcus is well developed, and an "Ursine lozenge" is more or less distinctly defined in front of it.

* Or *Galictis vittata*.

Fig. 6.

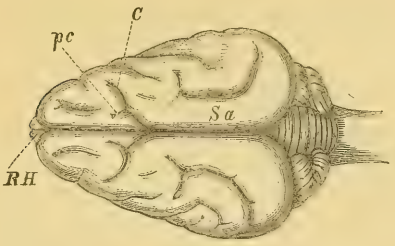


Fig. 7.

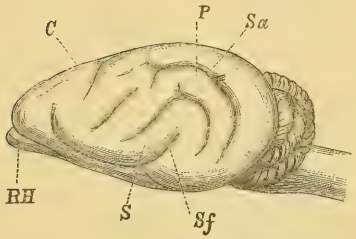


Fig. 6. Dorsal surface of brain of *Grisonia*, natural size. *C.* Crucial sulcus. *RH.* Rhinencephalon. *pc.* Precrucial sulcus. *Sa.* Sagittal gyrus.

Fig. 7. Lateral view of brain of *Grisonia*, natural size. *C.* Crucial sulcus. *P.* Parietal gyrus. *RH.* Rhinencephalon. *S.* Sylvian gyrus. *Sa.* Sagittal gyrus. *Sf.* Sylvian fissure.

Gulo.—The brain of this animal is only known to me through the description and figure of the cast of the inside of its skull given by Professor Gervais*. He says:—"Je n'y retrouve pas, du moins sur le moule intra-cranium, le dédoublement des deux circonvolutions supérieurs caractéristiques du *Galictis barbara*."

The cast shows signs of the presence of an "Ursine lozenge," which seems to be much elongated antero-posteriorly; also of a greatly expanded and convoluted anterior limb to the sagittal gyrus, as well as of a longitudinal grooving of its middle and hinder part. I can say nothing, of course, as to the inter-relations between the hippocampal and sagittal gyri.

Mustela.—The Martens and Weasels† have that more simple

* See *l. c.* p. 145, pl. vi. fig. 7.

† See Leuret, *l. c.* p. 381, pl. vi.; and P. Gervais, p. 143, pl. vi. fig. 3 (intercranial cast); see also Krueg, *l. c.* pl. xxxvi.

condition of brain-surface which characterizes the smaller forms of each group of Mammals. Nevertheless, the three circum-Sylvian gyri are all distinctly present, though, as has been remarked by Professor Flower *, the sulcus separating the sagittal and parietal gyri is less produced posteriorly in them than it is in other species of Carnivora. They have, however, a long and oblique Sylvian fissure. The Sylvian gyrus seems generally to have its posterior limb the narrower. The parietal sulcus does not communicate with the sagittal, save at the ends of the, posteriorly short, sulcus which divides them. The sagittal gyrus is much the widest of the three circum-Sylvian gyri. There is a considerable crucial sulcus which is placed rather far back. In front of it there is either an unmistakable "Ursine lozenge," or a distinct trace of it. The crucial and calloso-marginal sulci unite.

Ictonyx.—The brain of the Zorilla has been well figured by Professor P. Gervais †. Its Sylvian fissure is long and oblique. The Sylvian gyrus is much narrower in front than it is behind the Sylvian fissure. The parietal gyrus is simple. The sagittal gyrus is wide, especially towards its anterior end. The crucial sulcus is large, and placed rather far back, a considerable, or moderate, part of the cerebrum lying in front of it. There is a distinct, but small, "Ursine lozenge;" and the hippocampal gyrus is divided from the sagittal by the junction of the calloso-marginal and crucial sulci. The sulcus which divides the parietal and sagittal gyri does not extend far backwards in this genus any more than in *Mustela*, ceasing near the posterior superior angle of the cerebrum.

Helictis.—The brain of this animal has been described and figured by the late Professor Garrod ‡. The anterior limb of the Sylvian gyrus is much the narrower; the parietal and sagittal gyri unite at the posterior superior angle of the cerebrum, as in *Ictonyx*. The calloso-marginal and crucial sulci unite and separate the hippocampal and sagittal gyri. There is a very distinct "Ursine lozenge," but it is open behind owing to the non-junction medially of the two halves of the crucial sulcus, each hippocampal gyrus rising to the surface in a most excep-

* P. Z. S. 1869, p. 482, note ‡.

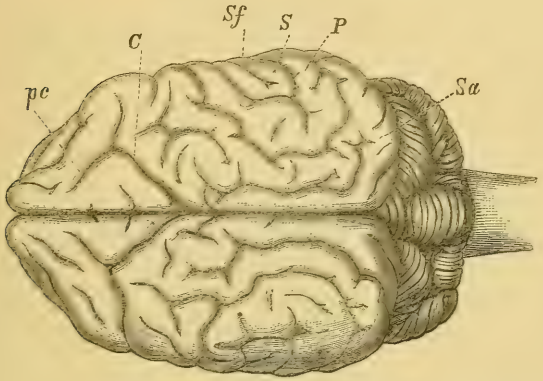
† See *l. c.* pl. ix. fig. 4; for a notice, see p. 144.

‡ See Proc. Zool. Soc. 1879, p. 307, figs. 1 & 2.

tional manner, and forming, on each side, the boundary of the median longitudinal fissure of the cerebrum.

Ursus.—The Bear's brain has been carefully described and admirably figured by MM. Leuret and Gratiolet *. I have examined the brains of nearly all the species, including that of the Sloth-Bear (*Melursus*). In all, the Sylvian sulcus has its anterior limb very much narrower than its posterior limb; in all, the parietal gyrus is simple and single; in all, the sagittal gyrus is very complex, and tends to become longitudinally divided into two; it is greatly expanded and much convoluted anteriorly. In all the

Fig. 8.



Dorsal surface of brain of *Ursus maritimus*, half natural size.
C. Crucial sulcus. *P.* Parietal gyrus. *pc.* Precrucial sulcus. *S.* Sylvian gyrus. *Sa.* Sagittal gyrus. *Sf.* Sylvian fissure.

species, the Sylvian fissure is exceedingly long and very oblique; and in all the hippocampal gyrus joins the sagittal gyrus, a bridging convolution dividing the crucial and calloso-marginal sulci. Finally, in the Bears we find present a large and very marked "Ursine lozenge," which in them attains its maximum of distinctness. It may be formed in different ways, either by secondary sulci proceeding forwards from the crucial sulcus, or by such sulci independently placed in front of it; and the condition may vary on the two sides of the same brain.

* See *l. c.* p. 375, pl. vi.; and P. Gervais, *l. c.* p. 134, pl. viii. fig. 10 (cast), and pl. ix. fig. 9 (brain itself); also Krueg, *l. c.* p. 635 and pl. xxxvii.; and Burt Wilder, *l. c.* fig. 10.

Lutra.—Three good figures of the brain of the Otter are given by Leuret and Gratiolet *, and it is also described and figured by Professor P. Gervais † and by Krueg ‡. These authors describe and represent the parietal sulcus as greatly broadening out anteriorly, and becoming connected by a "plis de passage" with the sagittal gyrus. In the specimens I have examined it seems, on the other hand, to be rather the sagittal which is enormously expanded towards its anterior end. The crucial sulcus is placed far back, but shows in front of it an unmistakable, though faintly marked, "Ursine lozenge." As in *Ursus* and certain other forms already mentioned, the anterior limb of the Sylvian gyrus is very much narrower than its posterior limb. The Sylvian fissure is very long, and extremely oblique in position. The hippocampal gyrus (according to Krueg) is separated from the sagittal by the junction of the crucial and callosomarginal sulci.

MM. Leuret and Gratiolet justly remark upon the possible deception which may arise as to the cerebral condition of an animal from an inspection of its skull only. The cranium of *Lutra* would seem to show that it is the hinder part of the brain which is specially enlarged, whereas the fact is that it is the anterior part of the brain which is relatively so augmented in volume.

Enhydra.—A cast of the interior of the skull of the Sea-Otter is figured and described by Professor P. Gervais §. It differs much from that of *Lutra* in that the crucial sulcus is placed more forwards, and the "Ursine lozenge" is much more conspicuous and relatively larger. The cerebrum seems to be very convoluted, the parietal gyrus expanding much anteriorly, and the middle of the sagittal gyrus being longitudinally grooved.

Thus the Arctoid Carnivora present us with cerebral characters by which they may be distinguished from the Canidæ (or Cynoidea) on the one hand, and from the Æluroidea on the other.

They differ from the first in not having four circum-Sylvian gyri, in not having the Sylvian gyrus subdivided, and in not having the posterior limb of the parietal gyrus bifurcating.

* See *l. c.* p. 382, pl. vi.
† *L. c.* p. 146, pl. ix. fig. 8.
‡ *L. c.* p. 631, pl. xxxvii.
§ See *l. c.* p. 146, pl. vi. fig. 9.

They also almost all differ from the Cynoidea by having generally a junction between the hippocampal and sagittal gyri, and, almost universally, by the possession of a precrucial "Ursine lozenge."

They also differ from the Æluroidea in that they have the "Ursine lozenge"; in that the anterior limb of the Sylvian gyrus tends to be, and very often is, much more slender than its posterior limb. They also differ from all non-feline Æluroids by mostly having a junction of the hippocampal and sagittal gyri behind the crucial sulcus. The Arctoids also differ from all other Carnivora by their tendency to a greater development in breadth and complexity of the sagittal gyrus.

The Pinnipedia.

The cerebrum of the Seals*, as is well known, is very different in aspect from any of the brains of the true Carnivora, whether the latter are purely terrestrial or more or less aquatic in their habits. It is generally more rounded in form and more richly convoluted, while the circum-Sylvian gyri are less distinct and easily defined, the parietal and sagittal sulci especially blending; moreover the crucial sulcus does not appear, when the brain is placed beside that of the true Carnivora.

Cystophora.—The brain of this genus is well represented in the collection of the Royal College of Surgeons. It shows a Sylvian fissure of moderate extent and somewhat vertical in position. The Sylvian gyrus is very complex and contorted, and joins the parietal gyrus by bridging convolutions, which are not constant in position. The latter gyrus ends abruptly a considerable distance behind the anterior end of the sagittal gyrus, which attains the front edge of the cerebral hemisphere and, as usual, surrounds the crucial sulcus. This latter sulcus is invisible, or all but invisible, when the dorsum of the cerebrum is looked at, owing to its being placed much further forwards than in any of the true Carnivora, namely quite at the anterior end of the cerebrum.

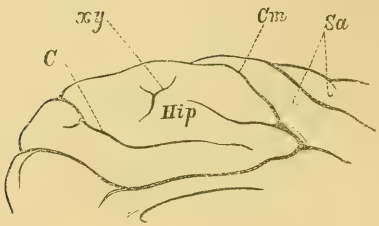
Phoca†.—In the brain of a Common Seal, which I had extracted for this paper, I found some very interesting conditions. Generally, the convolutions were like those of the form last noticed, and though a crucial sulcus could be detected at

* See Leuret, *l. c.* p. 390, pl. xi.; and Krueg, p. 642, and pl. xxxviii.

† See Leuret, p. 390, pl. xi.

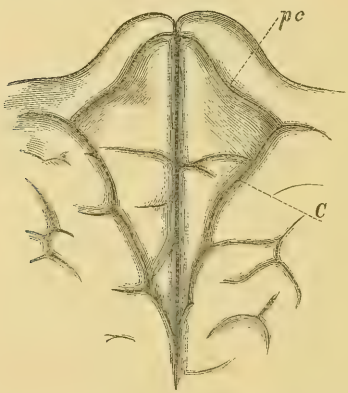
the anterior end of the cerebrum, there seemed at first to be no indication of an Ursine lozenge. By slightly separating

Fig. 9.



Vertical median section of part of the brain of *Phoca vitulina*, natural size.
C. Crucial sulcus. *Cm.* Calloso-marginal sulcus. *Hip.* Hippocampal gyrus. *Sa.* Sagittal gyrus. *xy.* Secondary sulci.

Fig. 10.



Dorsal surface of anterior median part of brain of *Otaria Gillespii*, natural size.
C. Crucial sulcus. *pc.* Precrucial sulcus.

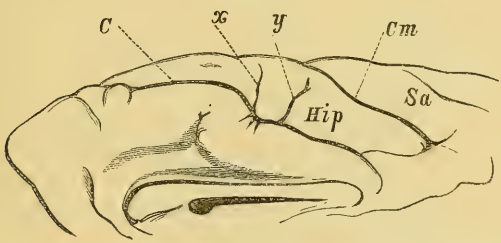
the cerebral folds, however, a small secondary, forwardly and inwardly proceeding sulcus could be detected on each side, so that a minute "Ursine lozenge" might be made out when the brain was viewed anteriorly.

A vertical section of the brain shows that the calloso-marginal sulcus is very widely separated from the inward prolongation of

the crucial sulcus, the very wide and voluminous hippocampal gyrus (grooved by secondary sulci *xy*) rising to the surface behind the crucial sulcus (fig. 9). The fold of cerebral substance thus interposed is far larger than any met with in even the Arctoid terrestrial Carnivora.

Otaria.—The brain of the Sea-Bear * is very instructive, for it supplies what would otherwise be a "missing link" of much importance between the brain of the Seals and that of the ordinary land Carnivora. In the first place it is intermediate in general form. It is less rounded than in the Seals, but differs from that of the ordinary Carnivora by being about as broad in front as it is behind. The Sylvian fissure is long (as in the Bears), but more vertical. The three circum-Sylvian gyri are much blended, and the whole cerebrum much convoluted. The parietal and sagittal gyri are very complex and extensively blended by bridging convolutions; they expand much anteriorly, and surround a very distinct crucial sulcus, which is here placed on the dorsum of the cerebrum (fig. 10). Moreover this crucial sulcus sends forwards converging secondary sulci which produce a very marked and unmistakable "Ursine lozenge" near the anterior end of the cere-

Fig. 11.



Median vertical section of part of brain of *Otaria Gillespii*, half natural size.

C. Crucial sulcus. *Cm*. Calloso-marginal sulcus. *Hip*. Hippocampal gyrus. *Sa*. Sagittal gyrus. *x* & *y*. Secondary sulci.

brum. The Ursine lozenge is distinct and large, and the crucial sulcus is very conspicuous. But for the distinctness of this lozenge in *Otaria*, I should probably have failed to detect the minute and obscure lozenge of *Phoca*; and thus the brain of *Otaria* is truly a link which it would have been unfortunate to

* This has been described and figured by Dr. Murie, F.L.S. See Trans. Zool. Soc. vol. xiii. pp. 519–527, pl. 78 & pl. 79. fig. 44.

miss. The calloso-marginal and crucial sulci are widely separated by a large hippocampal gyrus, which rises to the surface of the cerebrum (fig. 11). Nevertheless there is a deceptive appearance of junction between the crucial and calloso-marginal sulci by the uprising of an oblique secondary sulcus (*y*), which ascends from the hinder part of the backward prolongation of the crucial sulcus almost to that part of the calloso-marginal sulcus which joins the dorsal surface of the cerebrum.

Thus the cerebral characters of the Carnivora and Pinnipedia fully justify and confirm the inductions so long ago made by the late Mr. H. N. Turner *, and further worked out and improved by Professor Flower †. The cerebra of these animals group themselves, I think, unmistakably in four sets corresponding with the *Arctoidea*, the *Æluroidea*, the *Cynoidea*, and the *Pinnipedia*, though the brains of the *Viverrinæ* are so divergent through the atrophy of the crucial sulcus, that they may be held to constitute a fifth subordinate group by themselves. Do the facts here given throw any, and, if any, what, glimmering of light on genetic affinity and Phyllogeny?

The late Professor Garrod threw out the suggestion ‡ that the brain of the Dogs was a further and higher development of that of the Viverrine group, passing upwards through the Felidæ.

I cannot, however, any more than Professor Flower § or Professor Huxley, favour such a genealogical table of the Carnivora, on account of other, non-cerebral, anatomical considerations; but though I cannot regard this sketch of Professor Garrod's as happy phylogenetically, it appears to me to be a very correct one morphologically, and that his words express fairly well the morphological relations between the cerebra of the different groups of Carnivorous Mammalia.

There is a point, however, as to which the Carnivorous brain does appear to me to afford a solid ground for accepting a certain phylogenetic view. The Pinnipedia form a group so peculiar as to make their origin a question of some difficulty. The brain of the Seals is so divergent from that of the ordinary Carnivora, that MM. Leuret and Gratiolet separated it widely from the latter, relegating it ‖ to their eleventh mammalian group, and interposing the whole of the Ungulates and Edentates between

* P. Z. S. 1848, p. 86.
† P. Z. S. 1869, p. 85.
‡ See P. Z. S. 1878, p. 377.
§ See P. Z. S. 1880, pp. 75 & 76.
‖ See *l. c.* p. 371.

that eleventh group and their group of Carnivora. It has been often suggested that the Bears are the nearest existing allies of the Seals. There is, however, little in the anatomy of the true Seals to force conviction on us as to this matter; but when we turn to the brain of *Otaria*, we may, I think, therein read a very striking confirmation of the suggestion. The Arctoid group, and the Arctoid group alone of all Carnivora, possesses an "Ursine lozenge." That striking and exceptional feature is plainly to be seen (as herein pointed out) in the brain of *Otaria*. This circumstance, I venture to think, makes it very highly probable that the ancestor of the Pinnipedia was an Arctoid animal not very remote from the Ursine group of that extensive suborder.

In conclusion I desire to express my thanks to the authorities of the Royal College of Surgeons for the great facilities afforded me in studying the subject, and for their kindness in permitting drawings to be made from the specimens therein preserved.

On the Family *Arbaciadæ*, Gray.—Part I. The Morphology of the Test in the Genera *Cœlopleurus* and *Arbacia*.

By P. Martin Duncan, F.R.S., V.P.L.S., and W. Percy Sladen, F.L.S.

[Read 5th February, 1885.]

(Plates I. & II.)

Contents.

I. *Introduction.*

The Arbaciadæ of Gray, or the Echinocidaridæ of Desmoulins, have been studied, more or less, by nearly every naturalist who has investigated or classified the Echinoidea.

The embryology of species of the genus which gives the name to the family has been studied by A. Agassiz, Selenka, Busch,